Original Article

# Determinants of local and migratory movements of Great Lakes double-crested cormorants

Alban Guillaumet,[a] Brian Dorr,[b] Guiming Wang,[a] Jimmy D. Taylor 2nd,[c] Richard B. Chipman,[d] Heidi Scherr,[e] Jeff Bowman,[f] Kenneth F. Abraham,[f] Terry J. Doyle,[g] and Elizabeth Cranker[h]

[a]Department of Wildlife, Fisheries and Aquaculture, Mail Stop 9690, Mississippi State University, Mississippi State, MS 39762, USA, [b]United States Department of Agriculture/Wildlife Services/National Wildlife Research Center, Box 6099, Mississippi State, MS 39762, USA, [c]United States Department of Agriculture/Wildlife Services/National Wildlife Research Center, 321 Richardson Hall, Corvallis, OR 97331, USA, [d]United States Department of Agriculture/Wildlife Services, 1930 Route 9, Castleton, NY 12033, USA, [e]Center for Wildlife Ecology, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada, [f]Ontario Ministry of Natural Resources, Trent University DNA Building, Peterborough, Ontario K9J 7B8, Canada, [g]US Fish and Wildlife Service, 4401 N Fairfax Dr, MBSP-4107, Arlington, VA 22203-1610, USA, and [h]United States Department of Agriculture/Wildlife Services, 5757 Sneller Road, Brewerton, NY 10329, USA

We investigated how individual strategies combine with demographic and ecological factors to determine local and migratory movements in the double-crested cormorants (*Phalacrocorax auritus*). One hundred and forty-five cormorants were captured from 14 nesting colonies across the Great Lakes area and fitted with satellite transmitters. We first tested the hypotheses that sexual segregation, density-dependent effects, and the intensity of management operations influenced home range size during the breeding season. The influence of these factors appeared to be limited in part due to random variability in foraging and dispersal decisions at individual and colony levels. We also designed a statistical framework to investigate the degree and determinants of migratory connectivity. Our analyses revealed a significant migratory connectivity in cormorants, although we also observed a nonnegligible amount of individual variability and flexibility. Our data were most consistent with the existence of a migratory divide across the Great Lakes, with western populations using mainly the Mississippi Flyway and eastern populations the Atlantic Flyway. Previous and current studies suggest that the divide cannot be explained by past divergence in isolation, a way to diminish travel cost, or the Appalachians constituting an ecological barrier per se but is rather the consequence of the distribution of suitable stopover and nonbreeding areas. However, a parallel migration system and no migratory divide could not be entirely ruled out with present data. *Key words:* home range, management, migratory connectivity, migratory divide, parallel migration, satellite telemetry. *[Behav Ecol]*

## INTRODUCTION

Movements are key elements of the ecology and geographic distribution of animal species as recognized by the emergence of a new discipline called "movement ecology" (e.g., Holden 2006; Nathan et al. 2008). The advent of modern satellite tracking methods has facilitated research on movements and has shed new light into how individual strategies combine with demographic and environmental factors to determine specific movements such as foraging trips and seasonal migrations.

In this paper, we examined the local and migratory movements of a piscivorous colonial waterbird, the double-crested cormorant (*Phalacrocorax auritus*; hereafter cormorant). After a period of historical decline, the cormorant has recently undergone a dramatic recovery and expansion particularly in the interior of North America (Wires and Cuthbert 2006). This expansion has led to conflicts with aquaculture and recreational fishing and impacts to other natural resources such as conesting bird species and vegetation (Taylor and Dorr 2003). As a result, the control of cormorant populations

was progressively implemented on a local basis, starting in 1986 with depredation permits issued by the US Fish and Wildlife Service (USFWS 2003). Management techniques include harassment, nest destruction, and egg oiling (to prevent hatching and relaying) at nesting colonies, mainly in the Great Lakes area, and culling on the breeding grounds and aquaculture ponds in the southeastern United States where the interior population of cormorants winter (Taylor and Dorr 2003).

Many factors can influence foraging movements and home range size (HRS) in the interior population of the cormorant. Random variation between years, colonies, or individuals constitutes a first source of variation, as there is growing evidence that individuals within a population may vary considerably in the way they use habitat and resources (Cherel et al. 2009). Various social and ecological constraints can also affect individual strategies, leading to differential responses by individual attribute (e.g., age, sex, status, or condition) or population (e.g., colony or lake). For instance, sexual segregation is widespread in vertebrates (Ruckstuhl and Neuhaus 2005), and in the Columbia River Estuary, Anderson et al. (2004) found that male cormorants commuted nearly twice the distance to forage compared with females. Density-dependent disturbance or depletion of prey around breeding colonies may lead to an increase in the home range as suggested by studies of northern

gannets (Lewis et al. 2001) and of different species of cormorants and shags (Ridgway et al. 2006). Finally, human-related disturbance may affect animal's behavior and home range (Pope et al. 2007). In the nonbreeding range of cormorants, Scherr et al. (2010) suggested that the greater home range of individuals wintering near aquaculture facilities was a consequence of harassment campaigns around the ponds.

Recent studies also suggest that migratory species may have highly flexible migratory strategies, not only at the population level but also at the individual level (Quillfeldt et al. 2010). Oppel et al. (2009) suggested that random variation between individuals was the most important factor predicting winter movement decisions by king eiders. Berthold (2001) indicated that in northern bird species, males may winter farther north than females. Scherr et al. (2010) did not find difference in latitude between wintering male and female cormorants; however, cormorants were marked only from Georgian Bay, in the North Channel of Lake Huron, Ontario.

Migratory connectivity is the degree to which a specific breeding population can be linked to a specific wintering location. Unraveling the degree of migratory connectivity in the cormorant is important to develop efficient management strategies on a local and regional basis (Green et al. 2006). There is also an ongoing debate whether cormorant populations should be managed on a flyway basis (Hebert et al. 2008).

Three different migratory scenarios could apply to Great Lakes cormorants (see Supplementary Material, Supplementary Appendix 2.1 for further details): 1) no migratory connectivity, corresponding to random individual decisions. The available banding data suggest "considerable mixing and overlap in winter" (Dolbeer 1991); however, band returns do not provide any insights into the actual routes followed by migrating birds. Consequently, whether different cormorant breeding populations tend to follow different migratory routes is currently unknown. 2) A parallel migration system in which all individuals tend to follow the same migratory orientation, so that no subpopulations with alternative strategies can be identified (also called

broad-front migration by Berthold 2001). Faaborg et al. (2010) suggested that neotropical migrants tend to migrate in broad fronts across the landscape. 3) A flyway migration system, in which individuals from either side of a migratory divide congregate along 2 distinct migratory and/or wintering areas. In this case, the Atlantic and Mississippi Flyways taken as separate biological corridors rather than contiguous administrative units (e.g., Zimpfer and Conroy 2006). The Appalachian Mountains, which may constitute an unsuitable intermediate migratory corridor for cormorants, are a good candidate for generating such a migratory divide (Brooks 1952; Fuller et al. 1998).

In this paper, we used 145 cormorants captured from 14 nesting colonies across the Great Lakes and fitted with satellite transmitters to study the determinants of local and migratory movements of Great Lakes double-crested cormorants. In the first part, we present a thorough case study of the factors underlying HRS during the breeding season. Specifically, we tested the hypotheses that sexual segregation, density-dependent effects, the intensity of management operations, and random variation between individuals, colonies, or years influenced the HRS during the breeding season. In the second part, we developed for the first time (to the best of our knowledge) a statistical framework capable of identifying the migration system that best fits the migratory movements of a species. The application of this framework to the cormorant suggested the existence of a previously undetected migratory divide across the Great Lakes. Besides direct implications for the management of threatened or overabundant species, this method can also address fundamental questions about the evolution of migration systems in birds.

## MATERIALS AND METHODS

### Home range size

One hundred and nineteen cormorants were captured from 9 colonies (variable = colony) in the Great Lakes area (Figure 1) during springs (from 3 May to 1 June) from 2004 to 2007 (variable = year). Cormorants were captured using modified

**Figure 1**
Raw GPS telemetry data. Tracks of 119 double-crested cormorants fitted with GPS transmitters in 2004–2007 at the following colonies (number refers to sample size): Four Brothers Is D (FB) and Young Is (YI) in Lake Champlain (purple, except # 40 from FB in black); Crossover (CR) and Blanket Is (BI) on the St Lawrence River (pink); Oneida Lake (ON) and Little Galloo (LG) in Lake Ontario (red); North Breakwater at Buffalo Harbor (BH) in Lake Erie (green); St Martin Shoal (SM) in Lake Huron and Green Is (GI) in Lake Michigan (blue). Symbol Is = Island. Bird # 40 (Black) is an example of loop migration, with 2 fall migrations using the Atlantic Flyway and 1 spring migration along the Mississippi Flyway. Time interval between recordings being variable, the line between 2 subsequent recordings is not necessarily the actual path.
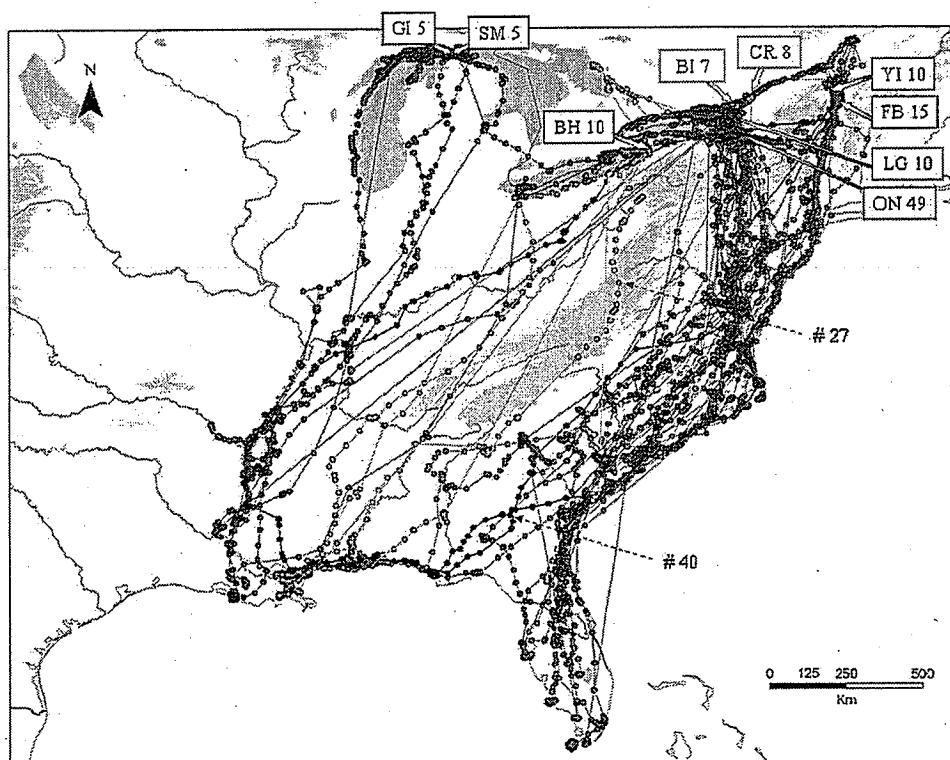
padded foothold traps placed in or near active cormorants nests (King et al. 2000). All 119 cormorants were fitted with a platform terminal transmitter (PTT), either a 45-g (2004) or 30-g (2005–2007) PTT-100 GPS capable solar rechargeable transmitter (Microwave Telemetry, Inc., Columbia, MD) using a backpack harness (King et al. 2000) and released at the capture location. Positional accuracy of these PTTs was ±18 m (http://www.microwavetelemetry.com/bird/solarArgosGPS.cfm). Transmitters were programmed to transmit either once hourly or once every 2 h (see Supplementary Material, Supplementary Appendix 1.1 for details).

## Home ranges and influencing factors

For the interior population of cormorants, the annual cycle can be roughly divided as follows (Hatch and Weseloh 1999, personal observation): the wintering period (December–March), the spring migration (March–May), the breeding season including incubation (May–July) and young rearing (June–August), and fall migration (August–December). Fall migration is often preceded by some postbreeding dispersal away from the breeding colonies (Figure 2). During this period, cormorants may use one or several different staging areas.

Following Breed et al. (2006), data for each bird were extracted on a monthly basis (variable = month), provided that sample size for the month (variable = nr) was considered sufficient for analyses (we used a minimum of 30 records, see Girard et al. 2002). HRS, defined as the area visited by a cormorant during a given month, was estimated using 95% minimum convex polygons (Mohr 1947) (variable = mcp). Alternative methods, including kernel density estimation, were implemented to evaluate the robustness of results (see Supplementary Material, Supplementary Appendix 1.1).

Nest counts ($N$) and management data collected under the Public Resource Depredation Order (hereafter PRDO) and Scientific Collecting Permits (SCCL) were used to assess the influence of colony size and management operations at nesting colonies. First, we calculated the variable called nests as $\sqrt{N}$ because a theoretical model predicts a positive linear relationship between travel distance to collect food and the square root of colony size (Lewis et al. 2001). Second, indices of management intensity were measured monthly for each colony as follows: $p\_cul$ was the total number of birds culled divided by 2 times the nest count, $p\_oil$ was calculated as $\sum_{i=1}^{n} n\_oil_i/N$, and $p\_nd$ as $\sum_{i=1}^{n} n\_nd_i/N$, where $n\_oil_i$ (resp. $n\_nd_i$) is the number of nest oiled (resp. destructed) during management session $i$. To account for a possible lag between management operations and a change in movement patterns, we also included values of $p\_oil$, $p\_nd$, and $p\_cul$ for the previous month (e.g., for HRS estimated in June, we included both $p\_oil\_5$ and $p\_oil\_6$). We acknowledge that some disturbance may not have been reported under the PRDO and SCCL, so our estimate of the impact of management must be regarded as conservative. Finally, 100 birds could be sexed (variable = sex) using a combination of genetic and morphometric methods (see Supplementary Material, Supplementary Appendix 1.1).

## Home range statistical analyses

We limited the HRS analysis to June because: 1) most management operations were conducted in May and June and 2) many birds were captured in late May or early June, so that the sample size is greater in June.

The factors affecting HRS were investigated with linear mixed models using mcp (95% minimum convex polygons) as the response variable. Prior to analysis, mcp was log
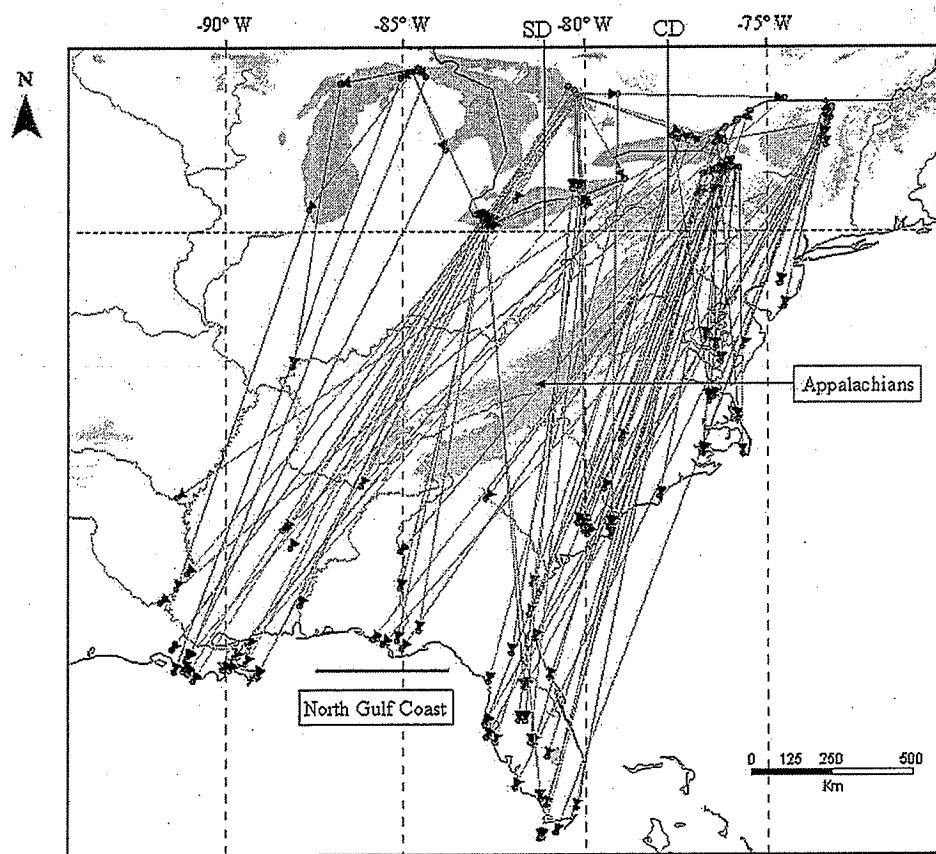


**Figure 2**
Migratory movements for 83 cormorants. Seventy individuals had data for November (Table 1). Thirteen had either stopped transmitting after October, after starting their southwards migration, or had missing data for November. Movements were divided in 2 segments characterized by arrows. The first segment (above the horizontal black dashed line) is displacement between the capture colony and the LGLSA. The second segment is the displacement between the LGLSA and the southernmost winter position (Smost). Some transmitters failed early, so that Smost may be a transitory position during migration (November–January positions are provided in Supplementary Material, Supplementary Appendix 2.4). Solid black vertical lines are estimates for the position of the migratory divide based on colonies (CD) or staging area (SD). Colony color scheme is as in Figure 1, except for the addition of birds from Georgian Bay (GB, olive–green); sample size: GB = 26, FB = 9, YI = 5, CR = 4, BI = 3, ON = 24, LG = 2, BH = 4, SM = 3, GI = 3.

transformed and 1 outlier was removed by only keeping values within ±3 standard deviation (SD) of the mean (for data normalization). Colony and year were treated as random factors, whereas sample size (nr), sex, colony size (nests), and management variables ($p\_oil\_6$, $p\_nd\_6$, $p\_cul\_6$, $p\_oil\_5$, $p\_nd\_5$, and $p\_cul\_5$) were treated as fixed factors (covariates). The latter were standardized (mean = 0, SD = 1) prior to analyses. For the sake of simplicity and a lack of a priori biological expectations, we did not consider potential interactions between explanatory variables for HRS (and migratory connectivity) analyses. Model selection was conducted using the REML.IC procedure (e.g., Bondell et al. 2010; see Supplementary Material, Supplementary Appendix 1.1 for details). We also measured the contribution of selected factors to the goodness-of-fit as measured by $R^2_{COR}$, the squared sample correlation coefficient between observed and predicted values (Byrnes and Stachowicz 2009).

For a few birds, we obtained tracking data for more than 1 year. As the sample size was too small to include a random "individual" factor, only the first June month was considered. However, as we were interested in individual effects, we compared HRS for June and July using 2 approaches: 1) A simple linear regression for the Oneida lake colony in 2005 and for all colonies and years considered together and 2) restricted likelihood ratio tests (RLRT) based on 10 000 simulations (Scheipl et al. 2008) to test whether the variance of a random effect was null in a model where mcp was explained by year, colony, and individual, treated as random factors.

## Migratory connectivity

To obtain a more regular sampling of colonies along the longitudinal gradient, we augmented our data set by including 26 birds captured from 5 different colonies in the Georgian Bay (Figure 2), which were equipped with Doppler-located PTTs for another study (Scherr et al. 2010). Although the accuracy of these PTTs is lower (sometimes greater than 1000 m), the difference is negligible compared with the scale of migratory movements (Figures 1 and 2).

Because of the duty cycle of non-GPS PTTs (1–2 positions every week outside the breeding season; Scherr et al. 2010), we could not follow the routes used by migrating birds equipped with non-GPS PTTs with the same precision as GPS-equipped birds. Accordingly, we collected for each bird (whenever possible) the following variables, compatible between sources: coordinates (latitude, longitude) of the capture colony (lat_col, long_col), coordinates of the last available staging area in the Great Lakes (hereafter, LGLSA), before the bird started its southward migration (lat_stag, long_stag), and coordinates of the bird along its migratory journey and overwintering period as estimated by the last available position of the bird in November, December, and January (e.g., lat_11, long_11). In November, the last available position was recorded only if the bird was south of its capture colony, at a distance ≥200 km.

## Statistical analyses for longitudinal distribution

The first step of our statistical framework is to calculate the position of the potential migratory divide. The binary variable flyway_col was designed to regroup the colonies using the Mississippi Flyway (taking the value 0) and the Atlantic Flyway (1). This variable predicted that all colonies lying on the same side of a divide would share the same migratory behavior, that is, using the Mississippi Flyway for colonies west of the divide or using the Atlantic Flyway for colonies east of it.

Because we had no a priori information concerning the location of such a divide, we developed an objective iterative procedure adapted from Guillaumet et al. (2008) to find the position of the divide that maximized the explanatory power of the variable flyway_col. The procedure was repeated independently for each month (illustrated here for November; see Supplementary Material, Supplementary Appendix 2.2 for more details). In the first step, only the easternmost colony was taken as part of the Atlantic Flyway (flyway_col = 1), whereas the remaining 13 colonies were treated as part of the Mississippi Flyway (flyway_col = 0). We calculated the second-order correction of Akaike information criterion (AICc) of the linear model where the longitude in November (long_11) was explained by flyway_col. In the second step, the easternmost of the 13 remaining colonies was now added to the Atlantic Flyway, whereas the remaining 12 colonies were still part of the Mississippi Flyway. We recalculated the AICc of the model where long_11 was explained by (the modified) flyway_col. This procedure was repeated until only the westernmost colony was part of the Mississippi Flyway. For subsequent analyses, we used for flyway_col the grouping that yielded the lowest AICc. The longitudinal position of the divide was calculated as the average between the longitude of the westernmost colony included in the Atlantic Flyway and the easternmost colony included in the Mississippi Flyway.

Because some birds made important longitudinal displacements during postbreeding dispersal (Figure 2), we also tested the hypothesis that the position of the LGLSA, rather than the position of the colony, was determinant to decide which flyway a bird would be using. We used the same procedure to build a binary variable flyway_stag based on the LGLSA.

Linear models were used to investigate the migratory connectivity for each of the 3 periods (November–January). A parallel migration system predicts a positive linear relationship between the longitude of the colony (or LGLSA) and the longitude of migration or winter locations (Supplementary Material, Supplementary Appendix 2.1). A flyway system instead predicts that the longitude of migration or winter positions is determined by the position of the colony (or LGLSA) with respect to the migratory divide. Hence, the next step of our method consists in comparing the relative explanatory power of the parallel (long_col and long_stag) and flyway (flyway_col and flyway_stag) migration variables, while accounting for the latitudinal positions of the bird (using lat_col, lat_stag, and, in November, lat_11).

Model selection was conducted using a backward stepwise regression and AICc as stopping criterion (Venables and Ripley 2002). The results were compared with an information-theoretic approach: All 128 possible models (including between 0 and 7 explanatory variables) were ranked by rescaling AICc values in comparison with the model with the lowest AICc, and we calculated the Akaike weights (Burnham and Anderson 2001). The ability of our method to discriminate among alternative hypotheses and to deal with unbalanced sample size is demonstrated in Supplementary Material, Supplementary Appendix 2.3. Because of the lower sample size for sex, analyses were performed twice (with and without sex).

## Other analyses

Model selection was also performed for the latitudinal distribution. The latitude of migration or winter positions was tentatively explained by flyway and parallel migration variables, while controlling for the longitudinal positions of the bird.

A randomization test was used to test the null hypothesis that the actual migratory paths (between the colony and the migratory location as measured by the last monthly location for November–January) did not result in shorter migratory

distances than expected if the cormorants were choosing their migratory location at random (details in Supplementary Material, Supplementary Appendix 3.1). All analyses were performed with R version 2.7.2 (R Development Core Team 2008). A table summarizing all variables is given in Supplementary Material, Supplementary Appendix 3.2.

## RESULTS

### Home range size

Variation in June HRS was considerable, ranging from 0.1 to 42 277 km$^2$ ($n = 118$, mean $= 1937$, SD $= 5297$, 95% confidence interval [CI] $= 0.9–17$ 250).

The best random effects part of the model selected by AICc contained only colony (all results are detailed in Table A1.1 of Supplementary Material, Supplementary Appendix 1). There was a significantly positive relationship between HRS and sample size (nr) but only when the threshold for monthly sample size ($T$) was fixed at 30.

Global tests suggested that no candidate fixed effect factor should be retained in the best models (all $P \geq 0.70$). If we still proceeded with model selection, neither sex nor colony size (nests) were ever retained as an important predictor. The intensity of nest destruction in May ($p\_nd\_5$) was selected for $T = 200$ and maximum likelihood estimation, but it was not significant ($t$ value $= 1.51$), and its contribution to goodness-of-fit was minimal (gain in $R^2_{COR}$ was ~0.006, from 0.241 to 0.246).

Consistent interindividual differences (comparison between HRS in June and July) were suggested by the results of simple linear regressions, both for the Oneida Lake colony in 2005 ($t = 3.78$, df $= 21$, $P = 0.001$) and for all colonies and years considered together ($t = 5.37$, df $= 100$, $P < 0.001$) and by an RLRT that accounted for the clustered structure of the data (RLRT $= 10.76$, $P < 0.001$). The latter also demonstrated significant intercolony differences (RLRT $= 19.40$, $P < 0.001$) but not interannual differences (RLRT $= 0$, $P = 1$).

### Migratory connectivity

#### Longitudinal distribution

Our procedure to fit migratory divides yielded consistent results across periods. The longitude of a divide based on breeding colonies was consistently estimated at $-77.64$, whereas the longitude of a divide based on staging areas was

**Table 1**
Migratory connectivity: model selection for the longitudinal distribution

| Response | $n$ | $R^2$ | Variable | $t$ | $P$ |
|---|---|---|---|---|---|
| long_11 | 70 | 0.54 | long_col | 2.96 | 0.004 |
| | | | flyway_stag | 3.41 | 0.001 |
| | | | lat_11 | 2.70 | 0.009 |
| long_12 | 58 | 0.36 | flyway_stag | 3.64 | <0.001 |
| | | | flyway_col | 2.12 | 0.038 |
| long_1 | 49 | 0.37 | flyway_stag | 2.74 | 0.009 |
| | | | flyway_col | 2.23 | 0.031 |

Stepwise regression results for the longitudinal distribution in November (long_11), December (long_12), and January (long_1). An information-theoretic approach yielded the same best model in all 3 cases (Table 2). For each month, we give the sample size ($n$), coefficient of determination ($R^2$), explanatory variables included, and the corresponding $t$ and $P$ values. The variable long_col = longitude of the colony, flyway_stag = 2 migratory flyways, with a divide based on the LGLSA, lat_11 = latitude in November, and flyway_col = 2 migratory flyways, with a divide based on breeding colonies.

estimated at $-81.12$, except in December (Figure 2, Supplementary Material, Supplementary Appendix 2.2).

For all 3 periods (November, December, and January), stepwise regression and an information-theoretic approach yielded the same best model (Tables 1 and 2). Sex never entered the best or the most parsimonious models when it was included in the analysis (not shown). In November, model selection suggested the combination of a parallel migratory orientation from the colonies (long_col) and a 2-flyway strategy depending on the last Great Lakes staging area (LGLSA) (flyway_stag). Birds on the Atlantic Flyway were on average farther north during November than birds on the Mississippi Flyway (lat_11).

In December and January, the same model including flyway_col and flyway_stag was selected (Table 1). Because the estimated position of the divide differed for colonies and staging areas, the inclusion of these 2 variables in the model suggested that each bird adopted one of the following strategies relying on geography. Birds on the Atlantic Flyway for both colonies (flyway_col = 1) and staging areas (flyway_stag = 1) used essentially an eastern migratory flyway, birds on the Mississippi Flyway for both colonies and staging areas used essentially a western flyway, and birds on intermediate locations (ascribed to the Mississippi Flyway for colonies but to the Atlantic Flyway for staging areas) had a mixed behavior, with a fraction of the birds using the western and another fraction using the eastern migratory flyway (Supplementary Material, Supplementary Appendix 2.5).

The information-theoretic approach confirmed the existence of migratory connectivity. Models that did not include at least 1 of the 4 parallel or flyway migration variables (long_stag, long_col, flyway_stag, and flyway_col) received very low statistical support (November–January, sum of Akaike weights, all <0.001). Alternative models (to the best model) had nonnegligible support. Between 3 and 5 models were within 2 AICc units (Table 2), although some are not truly competitive as they correspond to the best model augmented by an additional uninformative parameter (Arnold 2010).

The flyway variable flyway_stag stood out as the only explanatory variable present in all of the most parsimonious models (Table 2). The total Akaike weight for all models that include flyway_stag is near or superior to a 95% CI (97%, 98% and 86%, respectively for November–January). However, when flyway_stag was compared with parallel migration variables (long_stag and long_col) in a simple information-theoretic design (only 3 models compared, each with a single explanatory factor), the Akaike weight of flyway_stag was 0.90 in December, 0.61 in January, and 0.19 in November. Combining the flyway variables (flyway_stag and flyway_col) improved evidence for a flyway migration system, but the Akaike weight of parallel migration variables remained nonnegligible in November and January (e.g., in January, Akaike weight of long_stag was 0.12). A parallel migration system (and no migratory divide) cannot be entirely ruled out with these data.

#### Other analyses

Stepwise regression suggested only transient connectivity concerning the latitudinal distribution. No variable entered the best model in December and January, whereas in November, the only significant variable was the longitude (long_11), in agreement with the previous finding that birds on the Atlantic Flyway were on average farther north during November (Table 1).

The actual migratory distances were significantly less than expected under a scenario of random orientation (November–January, all $P < 0.001$). In December, for instance, the average distance covered was 1688 km, whereas the average of randomizations was 1716 km (95% CI $= 1700–1732$).

**Table 2**
Migratory connectivity: information-theoretic statistics

| Response | f_s | f_c | lo_s | lo_c | la_ | la_s | la_c | nv | np | AICc | $\Delta_i$ | $w_i$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| long_11 (n = 70) | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 3 | 5 | 374.46 | 0.00 | 0.21 | 0.54 |
|  | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 4 | 6 | 375.83 | 1.37 | 0.11 | 0.55 |
|  | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 4 | 6 | 376.43 | 1.96 | 0.08 | 0.54 |
| long_12 (n = 58) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 322.19 | 0.00 | 0.11 | 0.36 |
|  | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 4 | 322.42 | 0.23 | 0.10 | 0.35 |
|  | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 5 | 323.99 | 1.80 | 0.05 | 0.36 |
| long_1 (n = 49) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 271.64 | 0.00 | 0.10 | 0.37 |
|  | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 5 | 272.48 | 0.84 | 0.07 | 0.40 |
|  | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 4 | 6 | 272.97 | 1.33 | 0.05 | 0.42 |
|  | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 5 | 273.38 | 1.74 | 0.04 | 0.38 |
|  | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 4 | 273.55 | 1.91 | 0.04 | 0.35 |

Information-theoretic statistics of the most parsimonious models (within 2 AICc units) for the longitudinal distribution in November (long_11), December (long_12), and January (long_1). One hundred and twenty-eight models were fitted for each month (n = sample size), with explanatory variables either included (1) or not (0). The variable f_s = 2 migratory flyways, with a divide based on the LGLSA, f_c = 2 migratory flyways, with a divide based on breeding colonies, lo_s = longitude of the LGLSA, lo_c = longitude of the colony, la_ = latitude in November, December, or January, la_s = latitude of the LGLSA, and la_c = latitude of the colony. Symbol nv is the number of variables included, np is the number of parameters fitted, and $w_i$ is the Akaike weight.

## DISCUSSION

### Local movements

The HRS of Great Lakes double-crested cormorants during the breeding season was apparently not influenced by the sex of the bird, and the importance of colony size and management activities appeared limited (RESULTS, Supplementary Material, Supplementary Appendix 1.1–1.2). The rather unexpected absence of clear-cut effects may have been the consequence of a high random individual variability in movement decisions, as we found that the size of individual home ranges could be predicted from one month to the other. This interpretation also fits well with the high intraspecific variability evidenced in other waterbird studies (e.g., Adams et al. 2004; Takano and Haig 2004; Oppel et al. 2009).

Other factors may have contributed to the absence of clear-cut effects. In particular, we also found a high random variation between colonies. Inherent variability between colonies might explain the discrepancy between our study and the finding of a previous cormorant study in the Columbia River estuary (East Sand Island), where males commuted nearly twice the distance to forage compared with females (Anderson et al. 2004). Although such variability suggests differences in the proximity of suitable foraging areas around the colonies, the variation may also be due to differences in the proximity of preferred staging areas for birds making extended (≥1 day) trips outside the colony and for birds leaving their colony during the course of the breeding season (Supplementary Material, Supplementary Appendix 1.3).

An unknown fraction of these individuals may have failed in their reproduction, did not attempt to breed or attempted to breed in a different colony other than their capture colony, or simply explored alternative nesting colonies (Henaux et al. 2007). The fact that we did not have data to directly account for the breeding status (and its temporal variation) of the cormorants could have reduced our statistical power, although this is not likely. First, we anticipated that management activities would have increased the rate of breeding failure and colony desertion, and yet, management activities were not consistently associated with larger HRS in our analysis (Table A1.1 in Supplementary Material, Supplementary Appendix 1). Second, we made 2 attempts to account for the breeding status, in which we controlled for the time cormorants spent outside the colony or discarded the individuals that apparently deserted the colony (Supplementary Material,

Supplementary Appendix 1.2). These analyses showed a trend for a larger HRS in larger colonies and in colonies affected by management activities. However, none of the candidate variables was consistently included in the best models. When selected, candidate variables had a fairly small impact on the goodness-of-fit.

Although it is possible that our estimation of management effects is too conservative, we suggest that individual variation may be exacerbated in a species with strong dispersal capabilities, especially in a context where home range can encompass discrete waterbodies separated by variable distances, thereby offsetting any actual management or density effects. We suggest that future studies accounting for the breeding status may be helpful to estimate these effects with a greater accuracy.

### Migratory movements

We designed a statistical framework (Supplementary Material, Supplementary Appendix 2.1–2.3) to identify a putative migratory divide based on breeding or staging locations and to compare the explanatory power of a flyway migration system (based on the divide) with 2 alternative migration systems (no connectivity and parallel migration). Applying this framework to the double-crested cormorant, we found that the migratory scheme of Great Lakes populations is most compatible with the existence of a migratory divide, with western populations migrating west of the Appalachians and congregating in the lower Mississippi valley and eastern populations migrating east of the Appalachians and wintering in the Florida (also northwards, notably Carolina) wetlands (Figures 1 and 2). The bimodal orientation of birds from central colonies of the Great Lakes also brings support to the hypothesis of a migratory divide (Supplementary Material, Supplementary Appendix 2.5).

This is to our knowledge the first attempt to estimate the position of a migratory divide independently from the data and to rule out parallel migration, and one of the very few migratory divides to be documented for a North American bird species. Anderson and Anderson (2005) suggested the existence of 2 discrete flyways in the American white pelican, east and west of the North American Continental Divide. Other authors have reported the use of alternative flyways by different populations without characterizing the precise area of disjunction (Rubenstein et al. 2002; McKay 2009). In addition to a quantitative assessment of migratory connectivity, application of our method to other birds and migratory animals may reveal

further examples of migratory divides, bringing insights into the role played by geographic or climatic barriers in shaping within-species migratory strategies.

Because Great Lakes cormorant populations share a recent history of expansion and do not show genetic discontinuities (Waits et al. 2003; Green et al. 2006), the migratory divide evidenced here cannot be explained by past divergence in isolation and current populations retracing their historical expansion routes (Ruegg and Smith 2002). The hypothesis that it evolved to diminish travel cost or favor earlier arrival (Boulet and Norris 2006) also receives little support. Although the distances traveled were significantly shorter than expected if winter locations were chosen at random, the magnitude of the difference (average 28–48 km, only 2–3% extra flight) suggests that the distance traveled is not the primary force, especially when we compare this difference with the high within-flyway variance (Figure 2, e.g., Florida Keys vs. Carolina for the Atlantic Flyway).

Migratory divides may also be the consequence of ecological constraints such as unsuitable central migratory corridors (e.g., the Mediterranean Sea for the black stork: Bobek et al. 2008) or disjoint wintering areas, as in the red-billed quelea (Dallimer et al. 2003). For the cormorant, we suggest it is a combination of both. First, it seems likely that the intermediate nonbreeding area immediately south of the Appalachians (North Gulf Coast in Figure 2) is overall less favorable for the cormorant than the wetlands-rich Florida and Mississippi alluvial valley. This assertion may be supported by the fact that cormorants wintering in North Gulf Coast tend to be concentrated along the Apalachicola River System (around 85° west, Figure 2).

Second, cormorants do not appear to follow Appalachians ridges (Appalachian Flyway), unlike soaring raptors (Goodrich 1999), and rather travel either east or west of the mountains (Figure 1), as suggested by Fuller et al. (1998) for the Peregrine falcon. Although this may suggest that the cormorants are reluctant to fly over the Appalachians, we acknowledge that many birds were captured far enough east or west that they may not have flown over the Appalachians for other reasons (Figure 1). The vast majority of birds from intermediate breeding areas, which would have provided critical data, were birds from the Georgian Bay equipped with non-GPS PTTs. Unfortunately, the number of fixes obtained for these birds was insufficient to determine whether the fraction using the Atlantic Flyway circumvented the Appalachians by the east or west or rather flew over the Appalachians (see MATERIALS AND METHODS; but see also Supplementary Material, Supplementary Appendix 2.6). Increasing the number of GPS-equipped birds in this area may be required to address this issue.

We consider it unlikely the Appalachians constitute an ecological barrier to migration for cormorants per se. Evidence for this is suggested by the route taken by the individual # 27 (Figure 1) and by the fact that a large majority of cormorants from Oneida Lake crossed the Appalachians in the states of New York and Pennsylvania (88%, $n = 17$; Figure 1). It is notable that the Appalachians are only 300–500 m high in this area of crossover. Interestingly, 80% of them ($n = 15$) subsequently stopped in a productive coastal area, the Chesapeake Bay, for at least 24 h and generally longer periods of time (one of them even overwintered there; data not shown). We thus put forward for future research that a migratory divide in the Great Lakes is generated because the cormorants tend to avoid the Appalachian Flyway and the North Gulf Coast, mainly because there are fewer suitable stopover and nonbreeding sites.

Although we could safely reject the alternative that the migratory orientation is random within the Great Lakes (no connectivity hypothesis), it is worth noting here that a parallel migration system (and no migratory divide) could not be entirely ruled out with present data. More data from the central and western colonies of the Great Lakes may be helpful to refine our conclusions, and further studies may bring insights into the relative use of the Mississippi, Appalachian, and Atlantic Flyways among various taxonomic groups. Model selection also suggested a lack of sexual latitudinal segregation (although sample size precluded a definitive conclusion), and that birds on the Atlantic Flyway were on average farther north during November (Table 1), which also suggests that migratory characteristics of cormorants in the 2 flyways differed.

The existence of a significant migratory connectivity does not preclude an important individual variability already evidenced by banding data (Dolbeer 1991) and captured by the fact that the best models only explain about half of the total variance (Table 1). For instance, 1 bird from Oneida Lake used the Mississippi Flyway rather than the Atlantic Flyway and wintered in Louisiana, whereas at least 2 other individuals undertook a loop migration, using alternative flyway for the fall and the spring migration (e.g., Figure 1, bird # 40). Such a plasticity in migratory direction has also been evidenced in other migratory birds (Alerstam et al. 2006; Quillfeldt et al. 2010).

We conclude that both individual- and population-level strategies appear important to determine the local and migratory movements of interior populations of the double-crested cormorant. Future studies focusing on the nonbreeding season may characterize other sources of individual- and population-level strategies such as the utilization of freshwater versus marine resources (Hebert et al. 2008), natural versus anthropogenic waterbodies (Scherr et al. 2010), or the adoption of a nomadic versus sedentary behavior (Galvan 2005).

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/.

## FUNDING

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